THE ANATOMY OF *HETERODONTUS PORTUSJACKSONI* (MEYER, 1793).

PART I. THE NERVOUS SYSTEM.

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(Twelve Text-figures.)

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Introduction.

Although some scattered references occur in the literature on this subject, I am aware of no extensive work on the nervous system of *Heterodontus portusjacksoni* (Syn. *H. philippi* of authors) apart from that of de Beer (1924), whose research was carried out on embryological material, the largest embryo described being 70 mm. long. De Beer traced the development of the head with special reference to that of the skull, eye-muscles, nerves and blood vessels. Daniel (1934, p. 231, fig. 210) figures and comments on the brain of a closely allied species, *H.* (= *Gyropleurodes*) *francisci*, but does not give a detailed description of his material; judging mainly from his diagram, however, there are certain differences to be noted in the two species. Of further references on the sense organs in this shark, those of Garman (1888), Goodrich (1930), Allis (1919), and Norris (1929) are the most important and will be commented on in the appropriate section of the paper.

The supply of sharks has enabled me to make several dissections of this system, the largest specimen being more than three feet in length and in a good state of preservation.

The descriptions are grouped under two general headings—1. The Central Nervous System, comprising the brain and spinal cord, and 2. The Peripheral Nervous System, comprising the rest of the nervous system. Wherever it is possible the B.N.A. system of nomenclature has been used.

1. The Central Nervous System.

A. *The Brain.*

The brain is covered by two thin membranes or meninges. The outer one lies close to the wall of the cranial cavity and is very vascular—especially in the region of the anterior fontanelle. The inner membrane lies closely investing the brain and is separated by a considerable space, the perimeningeal space, from the outer one. The two meninges continue into the vertebral canal and stand in the same relation to the spinal cord as they do to the brain. They are connected, one to the other, in various places by fine strands of tissue.

The brain is divisible into three primary vesicles, the fore-, mid- and hind-brain, and to facilitate description the first and third of these two regions are further divided into two parts. The five divisions thus recognized (Fig. 1) from the anterior to the posterior are the telencephalon (TEL), the diencephalon (DIEN), the mesencephalon (MES), the metencephalon (MET), and the myelencephalon (MYEL).

The telencephalon and diencephalon together comprise the forebrain or prosencephalon. The telencephalon, as the name implies, forms the front part of the brain and is distinctly divided into two by a median anterior groove or sulcus. The separation of the two halves is not as marked in a large *H. portusjacksoni* as Daniel's figure shows for the closely related species *H. francisci*, but a dissection of the brain of a fairly young Port Jackson shark revealed that the furrow was very pronounced and that the pallial eminences were more marked than in larger specimens. Between the two olfactory tracts, on either side of the mid-line, is a prominent bulge caused by the median olfactory nucleus (M.O.N., fig. 2). From the sides of the telencephalon project the two olfactory lobes (OL.L., figs. 1, 2), which are continued forward as the olfactory tracts (OL.T., figs. 1, 2) to the olfactory bulbs (OL.B., fig. 5) which separate into two parts, one medial, the other lateral in position. At the posterior end of the telencephalon, on its dorsal surface, are the pallial eminences which are mound-like eminences and are well seen in a side view of the brain (P.E., fig. 1). In the centre of the dorsal surface of the telencephalon is a small round, cone-like pit, the recessus neuroporicus, which, in a well preserved specimen, is seen to contain blood vessels which enter the brain substance in this region (R.N., fig. 1).

From the ventral surface (fig. 2) the telencephalon is seen to be simple in structure—the two halves are separated by a median sulcus, about mid-way along which arise the terminal nerves (N.T., fig. 2). These are small, thread-like strands which run forward and outward from the sulcus to their ganglia which lie on the ventral surface of the telencephalon. From the ganglia, they join the olfactory tracts and run to the olfactory bulbs. On the floor of the telencephalon is the optic chiasma and the sides of this region form the thickened corpora striata in their lower region.

The diencephalon (DIEN, fig. 1) is only visible on the dorsal surface as a narrow region of the brain, without enlargements, situated just behind the telencephalon and in front of the optic lobes. It is characterized by the fact that on both the dorsal and ventral surfaces there are outgrowths—the pineal stalk and the infundibulum respectively. The pineal stalk (P.S., fig. 1) arises from the middle of the roof of the third ventricle, i.e., the cavity of the diencephalon. It is a long, thin strand of nervous tissue which runs dorsally towards the roof of the brain case. Its distal extremity is situated just behind the anterior fontanelle and is enlarged slightly to form the pineal body (P.B., fig. 1). The third ventricle can be seen when the telencephalon is pressed forward with the flat handle of a scalpel. There is a triangular opening leading into the cavity which lies below and which is roofed over by a thin membrane, plentifully supplied with blood vessels, called the anterior chorioid plexus. On the ventral surface of the diencephalon are the following outgrowths, the infundibulum and the two rounded lobi inferiores (INF.L., figs. 1, 2). On either side, also, is a balloon-like vascular sac, an outpushing of the infundibulum, the saccus vasculosus (S.VASC., fig. 2). The infundibulum meets and fuses with the hypophysis to form the pituitary gland.

The Pituitary Gland.

Though not composed of nervous tissue, the structure of the pituitary gland is included in this section of the paper because of its close association with the brain, to which it is connected through the infundibulum.

It depends from the floor of the diencephalon, and consists of three main portions: an anterior lobe which extends forward between the two lobi inferiores (ANT.L., figs. 1, 2), a very large ventral lobe (V.L., figs. 1, 2) which is attached dorsally to the anterior lobe by the neuro-intermediate part and extends downward to the floor of the braincase. The ventral lobe is strongly attached by tissues to the floor of the braincase and is hard to dissect out. A method which gave good results was to open the braincase and pour in about 10 c.c. of Bouin's fluid and allow the tissues to fix for fifteen minutes. Hardened in this way the pituitary could be removed easily in the whole state.

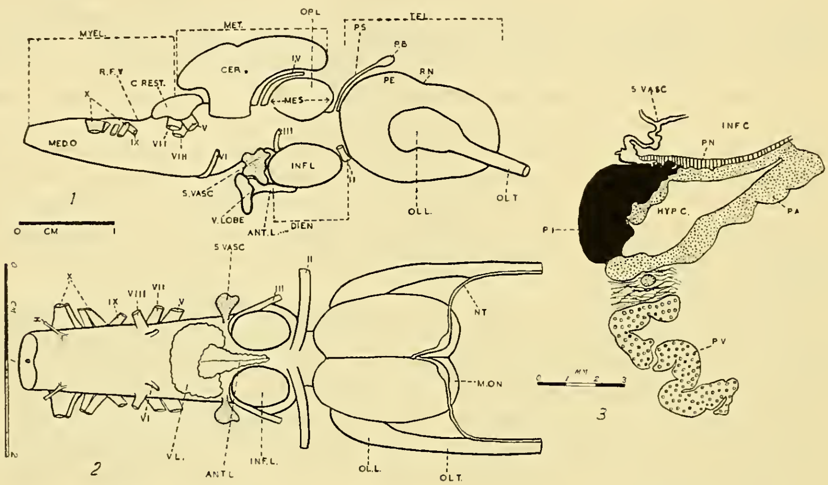


Fig. 1.—Side view of the brain of *Heterodontus portusjacksoni*.
ANT. L., Anterior lobe of pituitary; C. REST., Restiform body; DIEN., Diencephalon; INF. L., Lobus inferioris; MED. O., Medulla oblongata; MES., Mesencephalon; MET., Metencephalon; MYEL., Myelencephalon; OL. L., Olfactory lobe; OL. T., Olfactory tract; OP. L., Optic lobe; P.B., Pineal body; P.E., Pallial eminence; P.S., Pineal stalk; R.N., Recessus neuroporicus; R.F.V., Roof of IVth Ventricle; S. VASC., Saccus vasculosus; TEL., Telencephalon; V. LOBE, Ventral lobe of pituitary; I-X, Cranial nerves one to ten.

Fig. 2.—Ventral view of brain of *H. portusjacksoni*. (For explanation see legend to figure 1.)
M.O.N., Median olfactory nucleus; N.T., Nervus terminalis; V.L., Ventral lobe of pituitary; X, 1st Occipito-spinal nerve.

Fig. 3.—Longitudinal Section of Pituitary of *H. portusjacksoni*.
HYP. C., Hypophysial cavity; INF. C., Infundibular cavity; P.A., Pars anterior; P.I., Pars intermedia; P.N., Pars nervosa; P.V., Pars ventralis; S. VASC., Saccus vasculosus.

A median section of the pituitary (fig. 3) reveals the following structures: 1, A comparatively large hypophysial cavity (HYP.C., fig. 3), situated in the tissues of the pars anterior (P.A., fig. 3). The hypophysial cavity is larger in the sharks than in the rays according to de Beer (1926), and that of *Heterodontus* is large when compared with other sharks.—2, A small area composed of neuroglia fibres which lies just below the infundibular cavity (INF.C., fig. 3), penetrating the pars intermedia in parts and called the pars nervosa (P.N., fig. 3).—3, A pars ventralis (P.V., fig. 3); and a pars intermedia (P.I., fig. 3). The relative sizes and shapes of these parts are shown in figure 3.

The mesencephalon is hidden in a dorsal view by the forward growth of the cerebellum over the optic lobes. The latter can be seen well in a side view, however (OP.L., fig. 1) as paired, rounded outpushings of the roof of the mid-brain. The right and left optic lobes are separated from one another by a deep dorsal furrow. The cavity of the optic lobe, the optocoele, is of moderate size in *Heterodontus*.

The mid-brain is scarcely visible on the ventral surface of the brain. The sides of the mesencephalon are greatly thickened, leaving only a narrow aqueductus cerebri or aqueduct of the mid-brain, between the third and fourth ventricles, and these thickenings constitute the lateral fibre tracts. The third cranial nerve leaves the brain from the floor (III, fig. 1) and the fourth (IV, fig. 1) from the roof of the mesencephalon. The second or optic nerves leave the brain on the ventral surface of the diencephalon. Their fibres may be traced in the brain to the region of the optic lobes.

The rhombencephalon or hind-brain comprises two distinct regions, the metencephalon or cerebellum and the myelencephalon or medulla oblongata. The cerebellum (CER., fig. 1) is a dorsal, somewhat mushroom-shaped outgrowth arising from the roof of the hind-brain, extending forward over the mesencephalon and backward over the rest of the hind-brain which, like the mid-brain, is completely hidden from view. Dorsally the cerebellum is divided into right and left halves by a longitudinal furrow, while occasionally there is also present a less well-marked, transverse furrow at right angles to it. The cavity of the cerebellum is continuous with that of the medulla but is so small as to be almost obliterated.

The myelencephalon (MED.O., fig. 1) consists of those parts of the hind-brain posterior to the metencephalon or the cerebellum. Posteriorly, the myelencephalon merges insensibly into the spinal cord. Underlying the back of the cerebellum on the dorsal surface of the medulla are the restiform bodies (C.REST., fig. 1), raised, rounded thickenings of the roof in this part of the hind-brain. The cavity of the myelencephalon, the fourth ventricle, is covered over by a very thin roof which is plentifully supplied with blood vessels (R.F.V., fig. 1).

All the cranial nerves, back of the fourth, originate from the medulla oblongata.

B. *Spinal Cord.*

The spinal cord—the remainder of the central nervous system—extends from the medulla oblongata into the tail and reaches almost to its tip.

There are no marked dorsal and ventral grooves, and the shape in transverse section is that of an oval, slightly flattened on the ventral surface. The central canal (N, fig. 4) is circular in outline and is situated at approximately the centre of the grey matter. The shape of the grey matter is shown in section in figure 4. The dorsal rami (D.H., fig. 4) are not distinct as two arms, but merge together forming one dorsal mass. The ventral rami (V.H., fig. 4), on the other hand, are quite widely separated and there is a further, small, median ventral mass of grey matter in the mid-line between them (M.V.M., fig. 4).

2. The Peripheral Nervous System.

The remainder of the nervous system will be described under the headings of the Cranial and Spinal Nerves, the Sympathetic Nervous System and the Special Sense Organs.

A. *The Cranial Nerves.*

These nerves in *Heterodontus* are somewhat similar in origin and distribution to the usual elasmobranch type and differ only in small details due to the fact that the close approximation of the upper jaw cartilage to the skull and the consequent change in some of the muscle origins, has necessitated slight changes in the courses followed by the nerves which supply them. There is no otic branch to the facial nerve, a fact also noted by de Beer (1924*b*).

The first or olfactory nerve is purely sensory and arises as numerous short strands from the mucous membrane of the olfactory organ and passes backward as two short bundles to the olfactory bulb. According to de Beer (1924*b*) these two divisions of the olfactory nerve—the medial and lateral divisions—do not coincide with the two divisions of the olfactory sac. Fine nerve strands from the medial olfactory nerve bundle pass to the lateral part of the olfactory sac and vice versa. The olfactory bulbs are joined to the olfactory lobes of the brain by long, comparatively thick olfactory tracts (OL.T., figs. 1, 2, 5).

Easily seen on the ventral surface of a well-preserved brain are the two terminal or accessory nerves (T.N., fig. 2). They emerge from the floor of the telencephalon in the mid-line as two slender threads, the left one slightly in advance of the right. Each nerve runs outwards a short distance to a single, small ganglion, which lies on the ventral surface of the fore-brain towards its anterior end. De Beer (1924*b*) describes the development of the terminal nerve in this shark and in the last stage, namely 70 mm., which he figures, this nerve lies on the dorso-anterior surface of the fore-brain. In the adult it is, in all the cases I examined, on the ventral surface of the brain and its ganglion has left its position between the two divisions of the olfactory nerve (as described by de Beer in the 70 mm. stage) and now lies on the ventral surface. The adult condition is thus uniform with that of *Squalus* and *Amia*.

The optic nerve (II, figs. 1, 2, 5) originates in the retinal layer of the eye and is purely sensory in function. The fibres gather together and form a thick, round trunk, which passes through the sclerotic layer of the eyeball and runs across the orbit to pierce the wall of the braincase by the optic foramen. It forms a chiasma with its fellow of the opposite side and enters the diencephalon through its floor. The crossing of the nerves takes place just after they have entered the body of the diencephalon and is not visible externally.

The oculomotor nerve (III, fig. 1) emerges from the ventral surface of the mid-brain just behind the inferior lobe and runs dorsally, perforating the side-wall of the cranium above the mid-line of the orbit. On entering the orbit, the nerve splits into three branches. The most anterior branch follows a short course to the internal rectus muscle on which it breaks up into a number of small branches. The middle branch runs over the base of the internal rectus muscle and then divides into two branches which supply the superior rectus muscle. The remaining branch is the largest and supplies the inferior oblique and inferior rectus muscles. It runs first of all posteriorly, over the internal and superior rectus muscles, then passing under the external rectus and beneath the inferior rectus, to which it gives off a branch, it proceeds to the inferior oblique, which it also innervates. This deep branch gives off a fine twig which runs to the ciliary ganglion.

The fourth or trochlear nerve (IV, figs. 1, 5) arises from the dorsal surface of the mid-brain, just behind the optic lobes. It is a fine nerve which runs dorsally in the cranial cavity and perforates the cranial wall high up, in front of the optic foramen. It supplies the fibres of the superior oblique muscle.

The fifth or trigeminal and seventh or facial nerves arise close together from the side of the medulla oblongata, but the roots of the former complex are slightly anterior and below those of the facial nerve (V and VII, fig. 6).

The branches of the fifth nerve pierce the side-wall of the cranium through the orbital fissure, through which also passes the abducens or sixth nerve and also the superficial ophthalmic branch of the seventh nerve (R.O.S.VII, fig. 6). The relationships of the fifth and seventh nerves are shown in figure 6 and do not differ much from those pictured by de Beer (1924*b*) except that the two nerves and their ganglia are more closely associated in the adult than in the embryo.

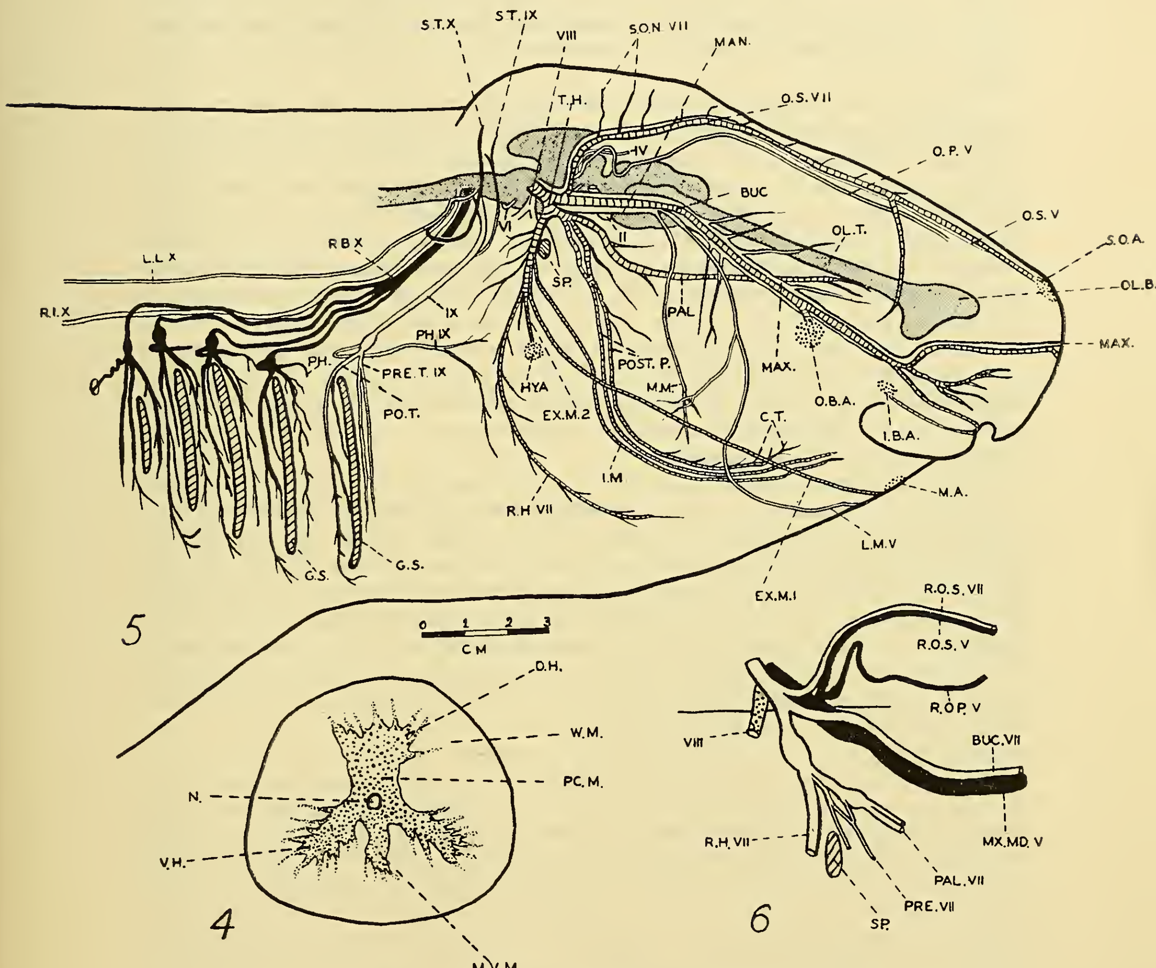


Fig. 4.—T.S. Spinal Cord of *H. portusjacksoni.*

D.H., Dorsal horn of grey matter; M.V.M., Median ventral mass of grey matter; N., Central canal; PC. M., Paracentral mass; V.H., Ventral horn of grey matter; W.M., White matter.

Fig. 5.—A Projection of the Sagittal Plane of the Cranial Nerves of *H. portusjacksoni.* The outlines of the brain are schematic.

BUC., Buccal branch of VII; C.T., Fine branches of palatine to oral epithelium; EX. M.1 & 2, External mandibular branches of VIIth nerve; G.S., Gill slit; HY.A., Hyoid ampullae; I.B.A., Inner buccal group of ampullae; I.M., Internal mandibular VII; L.L.X., Lateral line element of Xth nerve; L.M.V., Lateral branch of mandibular nerve; M.A., The main branches of the fifth nerve are four in number, namely, the superficial ophthalmic, the deep ophthalmic, the maxillary and the mandibular nerves.

1.—The superficial ophthalmic which is a mixed nerve (O.S. V, fig. 5) runs dorsally from its ganglion along with the nerve fibres of the superficial ophthalmic branch of the facial nerve. The two nerves continue forward through the orbit, lying close to and high up next to the outer side of the cranial wall. At the anterior end of the orbit these nerves pass through a tunnel in the cartilage and emerge on the dorsal surface of the skull and then run for some distance just beneath the skin towards the snout, giving off branches to the skin along their course.

2.—The deep ophthalmic (O.P.V., fig. 5), after leaving its ganglion, passes forward in the orbit as a fairly fine nerve. From the orbital fissure (for names of foramina in the skull see Daniel, J. F., 1934) it runs dorsally over the external rectus muscle, under the superior rectus muscle, and then turning forwards it runs near the back of the eyeball to which it gives off four small twigs. It passes between the two oblique muscles to the anterior wall of the orbit where it passes through a tunnel in the cartilage of the pre-orbital process just below the superficial ophthalmic, and emerges on the dorsal surface along with the latter. It supplies the tissues in this area, as well as the skin of the cheek region.

In the orbit, near the origin of the external rectus muscle, this nerve gives off a tiny branch of non-medullated fibres, the ciliary branch, which runs to the ciliary ganglion, where it is joined by a small branch from the deep branch of the oculomotor nerve. The ciliary ganglion gives off a branch which enters the eyeball and supplies the ciliary muscles.

3.—The maxillary nerve (MAX., fig. 5) arises from the Gasserian ganglion and passes in close association with the mandibular branch and the buccal branch of VII across the floor of the orbit to its antero-ventral corner. From here it runs with the buccal branch of VII forward across the cheek to the base of the olfactory capsule, but always lying deeper than the buccal branch. The nerve turns sharply medially and runs between the muscles and the back of the olfactory capsule till it reaches the outer side of the pterygo-quadrate cartilage. Here it turns forward and runs beside the upper jaw towards its symphysis with its fellow from the opposite side, giving off, throughout its course, branches to the tissue and muscles. These branches are represented in figure 5.

Mandibular ampullae; MAN., Mandibular branch of Vth; MAX., Maxillary branch of V; M.M., Medial branch of Mandibular V; O.B.A., Outer buccal group of ampullae; OL. B., Olfactory bulb; OL. T., Olfactory tract; OP.V, Deep ophthalmic of Vth nerve; OS.V, Superficial ophthalmic branch of Vth nerve; OS.VII, Superficial ophthalmic branch of VIIth nerve; PAL., Palatine branch of VII; PH., Pharyngeal branch of Xth nerve; PH.IX, Pharyngeal branch of IXth nerve; POST. P., Posterior branch of palatine VII; PO.T., Post-trematic branch of IXth nerve; PRE.T.IX, Pre-trematic branch of IXth nerve; R.B.X, Branchial division of Xth nerve; R.H.VII, Hyoid branch of VII; R.I.IX, Visceral branch of vagus; S.O.A., Supra-orbital group of ampullae; S.O.N.VII, Nerves to sense organs of supra-orbital canal; SP., Spiracle; ST.IX & X, Supra-temporal branches of the IXth and Xth nerves; T.H., Truncus Hyoideus; I-X, Cranial nerves 1-10.

Fig. 6.—Diagram of the Relations of the Trigeminal, Facial and Auditory nerves in *H. portusjacksoni.*

The Trigeminal nerve is black, the Facial white, and the Auditory is stippled.

BUC.VII, Buccal branch of the VIIth nerve; MX.MD.V, Maxillary and Mandibular branches of the Vth nerve; PAL.VII, Palatine branch of the VIIth; PRE.VII, Pretrematic branch of the VIIth nerve; R.H.VII, Hyoid branch of the VIIth nerve; R.O.P.V, Deep ophthalmic branch of the Vth nerve; R.O.S.V & VII, Superficial ophthalmic branches of the Vth and VIIth nerves; SP., Spiracle.

4.—The mandibular nerve (MAN., fig. 5) arises from the Gasserian ganglion and runs in close association with the maxillary and buccal branches to the antero-ventral border of the orbit where it curves sharply towards the ventral surface and divides into two branches. The medial of these two branches passes directly towards the ventral surface and runs just lateral to the pterygo-quadrate cartilage, under the muscles (M.M., fig. 5). It gives off many small branches which supply the adductor mandibulae muscle fibres.

The lateral branch of the mandibular curves over the main mass of the adductor and, passing between the muscles, runs to the ventral surface to innervate the skin of the lower jaw region (L.M.V., fig. 5) as well as the first superficial ventral constrictor muscle. A branch passes into the levator labialis inferioris muscle. Branches are also supplied to the levator maxillae and the first superficial dorsal constrictor muscle. The branches are small and are given off from the mandibular in the orbit but are not shown in the figures.

The sixth or abducens nerve (VI, figs. 1, 2, 5) arises from the myelencephalon almost in the mid-ventral line, just behind the region where the fifth and seventh nerves arise. The sixth nerve then runs under the fifth and seventh complex and passes through the cranial wall along with the fifth nerve to the external rectus muscle which it supplies.

The seventh or facial nerve emerges from the cranium through the hyomandibular nerve foramen, except for the superficial ophthalmic branch which, as already described, enters the orbit through the orbital fissure. Its relationships with the fifth nerve are shown in figure 6. This nerve is made up of two groups of fibres, one of which innervates the sense organs of the skin and the other comprises the facial nerve proper. The following branches supply sense organs: (1) the superficial ophthalmic, (2) the buccal and (3) the external mandibular.

The superficial ophthalmic branch (O.S.VII, fig. 5) arises from its ganglion and, emerging from the cranium through the orbital fissure, runs with the superficial ophthalmic branch of the fifth nerve over the dorsal surface of the muscles of the orbit to its anterior border, where it passes into a tunnel in the cartilage in the pre-orbital process, at a higher level than that of the deep ophthalmic V nerve. Throughout its course in the orbit, fine, thread-like branches (S.O.N., fig. 5) are given off and these pass through foramina in the cartilage roofing the orbit, to the sense organs of the supra-orbital sensory canal. Emerging on the roof of the cranium from the tunnel of cartilage in front of the orbit, the nerve runs forward towards the snout, lying under the supra-orbital canal which it supplies. It also innervates a group of ampullae, the supra-orbital group (S.O.A., figs. 5, 10, 11) situated under the skin on the tip of the snout. About half-way between the supra-orbital ridge and the snout, a branch is given off from the nerve; this runs forward and downward to supply the sense organs of the region of the sensory canal which curves round the side of the nasal capsule.

The buccal branch (BUC., fig. 5) runs across the floor of the orbit with the maxillary and mandibular branches of the fifth nerve. *Heterodontus* thus agrees with *Mustelus* (Allis, 1901) in that those three branches make up the truncus infra-orbitalis, whereas in *Squalus acanthias* (Norris and Hughes, 1920) only the buccal and maxillary branches do so. From the antero-ventral border of the orbit the buccal runs forward and downward across the cheek region and consists at this point of a number of fairly large bundles of fibres rather than one large trunk. Situated about midway between the orbit and the snout, lying just under the skin, is an encapsulated bunch of ampullae (O.B.A.) to which the buccal sends a large branch. On the distal side of these ampullae the buccal is considerably smaller and continues forward to the base of the nasal capsule, along with the maxillary nerve, and in this region curves inwards behind the olfactory capsule towards the pterygo-quadrate cartilage. It separates into two groups of fibres, one of which runs between the nasal capsule and the upper jaw and supplies the anterior extremity of the infra-orbital sensory canal, while the other group of fibres supplies the infra-orbital canal in the region of the superior oral fold, i.e., on the latero-ventral aspect of the olfactory capsule and also the inner buccal group of ampullae. In its passage across the orbit the buccal gives off small twiglets which innervate the sense organs of the infra-orbital canal. These branches are not shown in figure 5, but they are quite numerous.

According to de Beer (1924*b*), and from my own observations, there is no otic branch in *H. portusjacksoni*. *Heterodontus* is thus different from *Squalus*. Innervation of the spiracular sense organ is brought about by a fine branch of the buccal, given off in the posterior region of the orbit.

The hyoid trunk of the seventh nerve (T.H., fig. 5) is composed of a number of types of fibres, which may be classified as: (1) branches innervating the sensory canals and ampullae (e.g., external mandibular), which are therefore comparable with other nerves supplying the acoustico-lateral system; (2) visceral sensory fibres represented by the palatine and internal mandibular branch, and (3) visceral motor fibres which supply certain of the head muscles.

The hyomandibular trunk leaves the cranium and enters the orbit through a large foramen, placed low down and towards the back of the orbit. From here the nerve trunk runs outward and slightly backward, lying just underneath the oto-hyoid ligament for some distance. Numerous, fine, twig-like branches are given off from the main nerve trunk and supply the muscles in this region with motor fibres. The various branches and their destinations will now be described under the classification given immediately above, which is the most convenient.

1.—The external mandibular (EX. M. 1 and 2, fig. 5) supplies only sense organs of the skin and in *Heterodontus* has two main divisions. The nerve runs from the main truncus hyomandibularis outward behind the spiracle. About midway between the origin and insertion of the pterygo-quadrate levator muscle the two divisions separate, the one runs forward across the cheek just beneath the skin (EX. M. 1, fig. 5) and the more posterior branch, which is very short, continues to follow the line between the hyoid and mandibular arches (EX. M. 2, fig. 5). The former branch innervates the hyomandibular and mandibular sensory canals and also a knot of ampullae on the lower jaw situated just behind the inferior oral fold. The more posterior branch supplies the hyoidean group of ampullae which is situated outside the hyoid arch about half-way up the side of the head. This branch appears thus to terminate abruptly in this region.

2.—Visceral sensory fibres are represented by the palatine and internal mandibular branches of this nerve.

The palatine branch (PAL., fig. 5) of the truncus hyoideus is a very large branch leaving the main branch near the cranial wall. It is best displayed in *H. portusjacksoni* by disarticulating the pterygo-quadrate from the cranium and pulling the upper jaw slightly away from the latter. The various branches of the palatine can then be traced through the tissues lining the buccal cavity.

The palatine arises from the geniculate ganglion and runs forward and downward in front of the spiracle. It divides into two main parts, one of which (PAL., fig. 5), after passing round to the ventral surface of the cranium, runs forward medial to the ramus of the upper jaw, giving off branches to the dorsal oral epithelium. The posterior branch of the palatine immediately divides into two

(POST. P., fig. 5) and these two nerves run over the antero-dorsal wall of the spiracle, to the tissues of which a small pretrematic branch is supplied. The nerves then run down the medial surface of the pterygo-quadrate cartilage to the lower jaw where they curve forward and run, just below the teeth, towards the symphysis of the lower jaw cartilages. Throughout their course they give off small twigs (C.T., fig. 5) which supply the oral epithelium of the side walls and spiracular region and the lower jaw.

The internal mandibular branch (I.M., fig. 5) arises from the hyoid trunk ventral to the posterior palatine nerves. It runs downward towards the lower jaw, behind the spiracle and medial to the pterygo-quadrate cartilage. It lies almost parallel to the posterior palatines. On the floor of the mouth it runs forward between the basihyal and mandibular cartilages, terminating between the symphysis of the lower jaw cartilages.

3.—The hyoid branch (R.H.VII, fig. 5) constitutes the viscero-motor fibres of the hyoid trunk. Its fibres run in the hyoid trunk, closely associated with those of the external mandibular, behind the spiracle giving off, as already described, fine nerves to the muscles in this region. The nerve continues to follow the line of the hyoid arch on to the ventral surface where it runs forward. It supplies, in passing, the second superficial dorsal constrictor and both superficial ventral constrictors 1 and 2. In the orbit a small branch runs to the first superficial dorsal constrictor. This branch is not represented in figure 5.

The acoustic nerve (VIII, figs. 1, 2, 5) arises from the brain along with the hyomandibular branch of the seventh. The two nerves are closely bound up together and pass out from the brain through the cartilage of the base of the otic capsule. A very short distance from its ganglion which lies beneath the hyomandibular, the eighth nerve divides into two branches. The anterior one divides into two branches which supply the ampullae of the anterior and the horizontal semicircular canals. The other branch passes backward and outward, subdividing into a number of small branches which supply the ampullae of the posterior semicircular canal and the remaining regions of the ear.

The ninth or glossopharyngeal nerve (IX, figs. 1, 2, 5) arises from the brain posterior to the sixth nerve, from a slightly more lateral position and runs through the cartilage of the floor of the otic capsule where it forms a ganglion above the first gill-slit. Before it enters the ganglion, the ninth nerve gives off a small dorsal, supra-temporal branch (ST.IX, fig. 5) which innervates the anterior (sometimes called the temporal or post-orbital) part of the lateral line canal. There is given off from this supra-temporal a small twig which runs backward, but its destination could not be determined. It probably supplies pit organs which I have not been able to locate. These two branches constitute the dorsal ramus of the ninth nerve. Three branches arise from the ganglion and of these the most anterior, the pre-trematic (PRE.T.IX, fig. 5) runs, as two or three branches, side by side, to the anterior side of the first gill-pouch and innervates the hyoidean hemibranch. It lies beneath the mucous membrane of the gill filament. From the posterior side of the pre-trematic a small nerve is given off just ventral to the ganglion. This is the pharyngeal branch (PH.IX, fig. 5) and soon curls forward and supplies the integument on the roof of the mouth. This pharyngeal nerve gives rise to a branch which runs down the side of the pharynx internal to the hyoid arch under the mucous membrane and, I think, corresponds to the internal pretrematic branch described by Daniel (1934) for *Heptanchus*. A third branch arises from the ganglion, the post-trematic (P.O.T., fig. 5) which immediately divides into two main branches, one of which lies in a slightly more anterior position on the gill arch and gives off branches to the internal side of the arch. Both branches of the post-trematic run in the anterior hemibranch of the first holobranch. The longer of the two post-trematics continues on to the ventral surface of the gill arch, giving off twigs to the branchial muscles on the way, and finally continues on to the floor of the pharynx which it innervates.

The ninth nerve is a mixed nerve, containing both motor and sensory fibres. The posterior ramus of the post-trematic is mixed and supplies motor fibres to the muscles in this region and sensory fibres to the mucous membrane. The anterior ramus of the post-trematic is sensory, as is also the pharyngeal one.

The vagus (x, figs. 1, 2, 5) arises from the medulla oblongata by several large roots which on closer examination prove to be made up of several smaller nerves. These smaller roots are seven in number, the most anterior lying just above the root of the ninth nerve and the remainder along a line from this point to another point on the dorsal surface, just behind and beside the roof of the fourth ventricle (fig. 1). All the nerves from these roots pass together through a foramen in the cranial wall which lies at a higher level on the skull than that of the ninth nerve and is slightly posterior in position to the latter. On the outer wall of the cranium the vagus appears as three large bundles of nerves, closely bound together. From this bunch of nerves run three groups of fibres: (1) the ramus lateralis (L.LX., fig. 5) which supplies the lateral line sensory canal; (2) the branchial divisions (R.B.X, fig. 5) of the nerve which supply the gill region other than that supplied by the ninth nerve; and (3) the third or visceral ramus which runs to the gut (R.I.X., fig. 5). The most anterior group of fibres to leave the brain passes into the ramus lateralis. This nerve runs towards the tail, between the dorsal and the ventral longitudinal muscle bundles and just beneath the lateral line. It extends almost to the tip of the tail. Even in the foramen in the cranial wall these fibres are distinct from those of the other groups. A small branch is given off in this foramen which innervates part of the supra-temporal region of the sensory canal (S.T.X., fig. 5). Its course is through the posterior cartilage of the otic capsule. Throughout its length the lateralis gives off fibres to the sensory organs of the lateral line. From the cranial wall the lateralis runs outward and backward, touching the wall of the anterior cardinal sinus, and then runs between the dorsal and ventro-lateral muscle bundles.

The next group of fibres forms the branchial part of the vagus, the biggest division of the nerve. The branchial nerves are four in number and lie in the floor of the anterior cardinal sinus and their ganglia lie one above each of the last four gill-slits. From each ganglion nerves run to the gill tissues, similar in distribution and number to those of the ninth nerve, except for the fact that the pre-trematic branch is single. There is, therefore, a pre-trematic branch which runs to the anterior hemibranch of the second gill-pouch where it branches immediately behind the cartilaginous branchial rays and innervates this region. The second branch is the post-trematic which immediately divides into two and runs to the anterior hemibranch of the second gill (i.e., the posterior hemibranch of the second gill-pouch). Each branch runs in the gill tissues in the same manner as the corresponding branch of the ninth nerve. The third branch, the pharyngeal, differs from that of the ninth nerve in that, instead of running forward at once on to the roof of the pharynx, it first runs backward over the top of the inter-arcuales muscles and then curves forward and inward on to the pharyngeal roof. (The above remarks apply to the distribution of the nerves of the second gill-pouch, which is typical.)

There is a slight difference in the last or fourth branchial. A slender nerve is given off from the ganglion which runs through the foramen of the fifth and rudimentary sixth epi-branchial cartilage and so to the side wall of the oesophagus; here it subdivides into numerous tiny branches which run forward on the ventral wall of the oesophagus to the sinus venosus of the heart. These fibres, therefore, represent the cardiac portion of the vagus, the fibres having separated from the visceral branch in the region of the anterior cardinal sinus and running from there with the fourth branchial branch for a short distance.

The Visceral Branch of the Vagus.

The third group of fibres of the vagus, the ramus intestinalis, runs closely associated with the fourth branchial branch to the region of the third holobranch. Here it separates from the branchial and continues to run backward and then turns slightly towards the midline. It enters the body cavity and breaks up into three large branches which later subdivide still further and run to the oesophagus, stomach and other viscera.

B. *Occipito-Spinal Nerves.*

In *Heterodontus* there are three occipito-spinal nerves designated as nerves *x*, *y* and *z*, from anterior to posterior respectively (fig. 7, *x*, *y* and *z*).

The rootlets of the nerve *y* arise from the ventral surface of the medulla at the level of the more posterior roots of the vagus nerve and are similar in appearance to the sixth cranial nerve. The small nerve, *x*, is very tiny and therefore difficult to dissect, but it occurs a short distance in front of *y* and has a similar origin from the ventral surface of the medulla.

The nerve *y* runs under the vagus through the cartilage where it turns backward to join the nerve *z*, and these two run together to join the hypobranchial nerve.

The nerve *z*, in *Heterodontus*, does not appear to possess a dorsal root as in some other Elasmobranchs, and is like *y* in origin and size. It joins *y*, as mentioned above, and runs with the hypobranchial nerve.

C. *Spinal Nerves.*

Each spinal nerve is a mixed nerve and has a single, dorsal, sensory root and a ventral, motor root arising from the spinal cord. The ventral root arises from the cells of the ventral horn of the grey matter, while the dorsal root extends from the dorsal horn of the grey matter to the dorsal root ganglion which lies in the cavity of the spinal column, and from here nerve fibres pass outward through the wall of the spinal column to join those of the ventral root. The ventral root pierces the basidorsal cartilage and its corresponding dorsal root pierces the succeeding interdorsal cartilage; the ventral root thus lies in front of its dorsal root. The mixed nerve, which is formed by these two nerve-elements, runs outward to supply the tissues of the corresponding segment of the body. In the region of the dorsal and ventral unpaired fins, the spinal nerves send branches to their muscles. In the region of the neck and shoulder, the spinal nerves form plexuses, the hypobranchial and pectoral plexuses.

At the level of the 15th spinal nerve, in the region just above the lateral abdominal vein, the terminal twigs of this and succeeding nerves up to the 25th nerve are connected together to form a nervous collector system.

The hypobranchial or cervical plexus in *Heterodontus* is formed by the union of the occipito-spinales nerves *y* and *z*, and the first two spinal nerves. These nerves run closely bound together, nevertheless retaining their individuality, above the branchial region with the branchial branches of the vagus nerve. Behind the vestigial sixth branchial arch (Hawkes, 1906) this plexus turns sharply downward and, running in front of the pectoral arch, reaches the longitudinal hypobranchial muscles which it innervates by its various branches (HYP. P., fig. 7).

A small twig is given off posteriorly, which joins the third spinal nerve. The third spinal nerve runs close to the fourth one, following a course almost parallel to that of the hypobranchial nerve. It divides into two; one half runs to the hypobranchial region just anterior to the pectoral girdle, whilst the other half runs with the fourth, fifth and sixth spinal nerves through the foramen in the pectoral girdle to the muscles of the pectoral fin (see fig. 7, 3).

The third, fourth, fifth and sixth spinal nerves are not closely bound together, but they represent the pectoral plexus of other sharks since they run together through the pectoral girdle foramen to the muscles of the dorsal side of the fin (BR. P., fig. 7). The fifth and sixth nerves also display a slight degree of fusion, about half-way between the spinal column and the ventral surface. The spinal nerves, as far back as the fifteenth, run to the dorsal side of the pectoral fin. The pelvic fin (and, in the male, the clasper) is supplied by spinal nerves 23 to 37.

D. *Sympathetic Nervous System.*

This system in *Heterodontus* is represented in the head by the ciliary ganglion and nerves. The ciliary ganglion lies in the back of the orbit, low down between the rectus muscles and the eyeball. The nerves running to it have already been described (pages 416, 418). In the trunk there is a small but extensive sympathetic nervous system. The anterior part of this system is so closely associated with the chromophil bodies of the adrenal glands that it is difficult to distinguish between them. The posterior part of the sympathetic nervous system comprises a series of segmentally-arranged ganglia which are not associated with the chromophil bodies and which are not connected with one another in a chain (fig. 8).

The ganglia occur as two longitudinal series, lying one on either side of the dorsal aorta. The anterior ganglion is the largest and represents several fused ganglia. It receives three twigs from the spinal nerves and gives off sympathetic nerves, three in number, which run in the mesentery along with the coeliac axis to the viscera (SY. N., fig. 8).

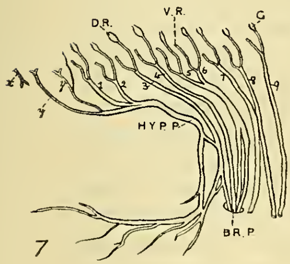
The posterior ganglia are small and extend back to the posterior region of the kidneys, to which they supply small twigs, as well as giving off branches to the posterior viscera and genital ducts.

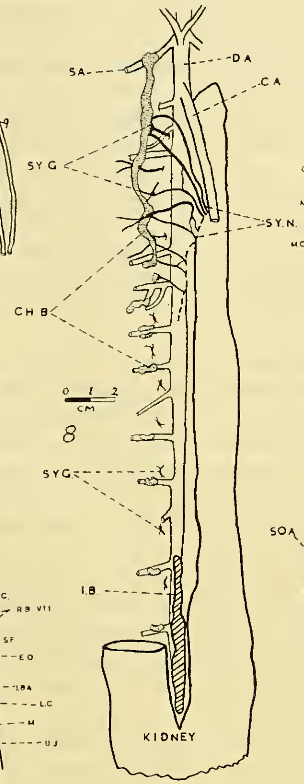
E. *Special Senses.*

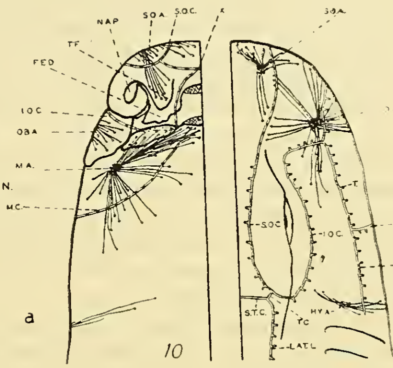
Under this heading the olfactory organ, organs of taste, the auditory organ, and the neuromast system will be described.

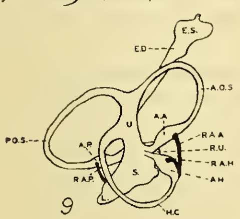
The Olfactory Organs.—The olfactory organs of *Heterodontus portusjacksoni* show an interesting difference from the structure found in a form such as *Heptanchus.* The incurrent nasal aperture is situated on the ventral surface, fairly near the tip of the snout (N.A.P., fig. 10A), while the excurrent opening leads backward on to the roof of the mouth, the angle between the axes of the two canals being about 70°. The opening of the excurrent canal is surrounded by a frill of dermal tissue (F.E.D., fig. 10A) which depends from a somewhat triangular fold of the upper lip (T.F., fig. 10A).

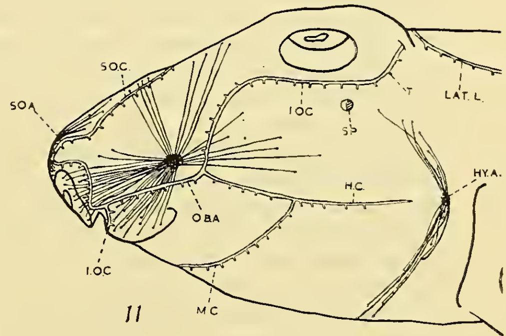
Allis (1919) has described the structures of the nasal organs of a heterodont shark, probably *Gyropleurodes francisci,* and a comparison showed that *Heterodontus portusjacksoni* has nearly similar structures, the differences being minor ones such as the shape of the openings of the nasal pit and the shape of the secondary upper lip. These differences are best shown by comparing figure 10A of this paper with figure 6, Plate 2, of Allis's paper and with his descriptions on pages 158–164.











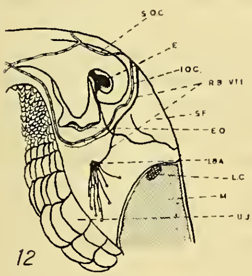


Fig. 7.—Diagram of the Occipito-spinal and First Nine Spinal Nerves. Viewed from Left Side.

BR.P., Brachial plexus; D.R., Dorsal root of spinal nerve; G., Ganglion of dorsal root of spinal nerve; HYP.P., Hypobranchial plexus; V.R., Ventral root of spinal nerve; *x*, *y* and *z*, The occipito-spinal nerves; 1-9, Spinal nerves 1-9.

Fig. 8.—Sympathetic Nervous System, Supra- and Inter-renal Bodies of *H. portusjacksoni* (right kidney removed).

C.A., Coeliac axis; CH.B., Chromaphil bodies (= medulla of adrenals of higher vertebrates); D.A., Dorsal aorta; I.B., Interrenal body (= cortex of adrenals of higher vertebrates); S.A., Sub-clavian artery; SY.G., Sympathetic ganglion; SY.N., Sympathetic nerves.

Fig. 9.—Right ear of *H. portusjacksoni* viewed from the outside.

A.A., Ampulla of anterior oblique semicircular canal; A.H., Ampulla of horizontal semicircular canal; A.P., Ampulla of posterior oblique semicircular canal; A.O.S., Anterior oblique semicircular canal; E.D., Endolymphatic duct; E.S., Endolymphatic sac; H.C., horizontal canal; L., Lagena; P.O.S., Posterior oblique semicircular canal; R.A.A., Branch of VIIIth nerve to ampulla of A.O.S.; R.A.H., Branch of VIIIth nerve to ampulla of H.C.; R.A.P., Branch of VIIIth nerve to ampulla of P.O.S.; R.U., Recessus utriculi; S., Sacculus; U., Utriculus.

The nasal cartilage in *H. portusjacksoni* is similar in all respects to that described by Daniel (1915) for *H. francisci* (= *Gyropleurodes francisci*). It does not form a complete ring and is not fused at any point with the nasal capsule, as Gegenbaur (1872) stated, but is merely attached to the latter by tissues.

The incurrent opening of the nasal aperture is pear-shaped with the broad end directed postero-laterally, and appears to be larger than that described by Allis in *G. francisci*. This opening leads into the nasal pit, which is quite large and somewhat reniform in shape. The excurrent canal leads backwards from the medial surface of the "kidney" to the roof of the mouth.

The outer layer of the oral and medial walls of the olfactory capsule is formed of a strong sheet of membraneous tissue, extending from the basi-trabecular cartilages, on the inside, across the floor of the capsule to join the tips of the nasal cartilage and the lateral edge of the nasal capsule. It is only interrupted where the excurrent opening of the nasal pit leads to the roof of the mouth. The median raphe of the folded, Schneiderian membrane lies parallel to the long axis of the incurrent nasal aperture. There are about 35 folds in the membrane on either side of the raphe.

The incurrent canal is separated quite effectually from the excurrent one by two flaps of tissue which overlap but do not fuse, the lateral one projects upward while the medial one hangs downward from the secondary upper lip.

The receptor organs lie in the Schneiderian folds and they send posterior fibres to the olfactory bulb, entering the latter as the true olfactory nerve.

Sensations received by the olfactory bulb are transmitted to the olfactory lobes of the brain by the olfactory tracts (OL.T., fig. 1) which pass back from the nasal capsule through the wide olfactory foramen.

Taste Organs.—There are numerous taste buds in the integument lining the mouth and pharynx where they occur on the roof, floor and sidewalls. They are more numerous towards the posterior part of these regions, especially at the back of the "tongue" process where they are only 3 mm. apart as opposed to 5 mm. at its anterior end. These organs are innervated by the visceral sensory fibres of the seventh and ninth nerves.

Auditory Organ.—The ear in *H. portusjacksoni* is housed in a strong, cartilaginous otic capsule on whose roof is the prominent post-orbital process of the

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Fig. 10.—Diagram of Cephalic Canals and Ampullae of Lorenzini in *H. portusjacksoni*. 10A, Ventral view; 10B, Dorsal view.

Ampullae represented by solid black dots, pores by open dots, and tubules by a line. F.E.D., Frill of dermal tissue below ex-current opening of nasal organ; H.C., Hyomandibular sensory canal; HY.A., Hyoidean group of ampullae; I.O.C., Infra-orbital canal; LAT.L., Lateral line canal; M.A., Mandibular group of ampullae; M.C., Mandibular sensory canal; N.A.P., Incurrent nasal aperture; O.B.A., Outer buccal group of ampullae; S.O.A., Supra-orbital ampullae; S.O.C., Supra-orbital canal; S.T.C., Supra-temporal canal; T., Tubule of sensory canal; T.C., Temporal canal; T.F., Triangular fold of upper lip; *x*. Point of junction of S.O.C. and I.O.C. in middle of upper lip.

Fig. 11.—Diagram of the Side View of Head showing Sensory Canals and Ampullae of Lorenzini. (For explanation see Figure 10.) SP., Spiracle.

Fig. 12.—Diagram of Roof of Mouth. Lower Jaw removed to show the Sensory Canals and Ampullae.

E., In-current opening of nasal organ; E.O., Ex-current opening of nasal organ; I.B.A., Inner buccal group of ampullae; I.O.C., Infra-orbital canal; L.C., Labial cartilage (cut); R.B.VII, Branch of buccal nerve VII; S.F., Superior oral fold; S.O.C., Supra-orbital canal; U.J., Upper jaw.

cranium. There are no external traces to indicate the positions of the various canals of the auditory organ. The ear consists of three semicircular canals with their ampullae and a saccular and an utricular region.

The anterior oblique semicircular canal (A.O.S., fig. 9) and the horizontal semicircular canal (H.C., fig. 9) have their ampullae at their lower and anterior ends, quite close to one another, and leading into the utriculus (A.A. & A.H., fig. 9). Near the junction of these two canals with the utriculus (U., fig. 9) is an opening from the latter into the sacculus, the recessus utriculi (R.U., fig. 9). The ampulla of the posterior oblique semicircular canal (P.O.S., fig. 9) does not join directly on to the utriculus. This ampulla is ventral in position and connects with the utriculus by a short canal (A.P., fig. 9).

The sacculus is not very large, and, from its posterior floor-region, a small, tongue-like sac, the lagena (L., fig. 9) projects obliquely outward and backward. The sacculus is continued dorsally on its medial side, into the endolymphatic duct. This duct is considerably larger where it opens to the surface of the head and forms an endolymphatic sac (E.S., fig. 9).

The various regions of the ear are all innervated by the eighth nerve which branches into two on leaving the brain case, each of these in turn giving rise to further branches. The anterior nerve and its twigs supply the ampullae of the A.O.S. and H.C. and is the smaller of the two; the larger, posterior branch supplies the ampulla of the P.O.S., the saccular region and the utricular region and also gives off a small branch to the lagena. The innervation is thus similar to that pictured by Daniel (1934, fig. 236 D, page 270) for *Heterodontus* (= *Gyropleurodes*) *francisci*, and the only differences lie in the size and shape of the sacculus and the endolymphatic sac.

Sensory Canal System.—The sensory canal system of this shark has been described and figured by Garman (1888) and that of a closely related species, probably *Heterodontus* (= *Gyropleurodes*) *francisci*, has been figured by Norris (1929), but since I cannot agree with the nomenclature used by the former and find a short temporal canal not shown by Norris I am including my own drawings and descriptions.

The lateral line canal extends from almost the tip of the caudal fin to the head region where it joins the supra-temporal canal (S.T.C., fig. 10B). Beginning almost at the tip of the tail as a closed canal (not, as Garman states, "a furrow"), the lateral canal runs forward, on a level just beneath that of the vertebral bodies of the vertebrae. This canal runs slightly dorsally and in the region of the base of the tail lies at the same level as the vertebral bodies. From here it continues forward at this level till it reaches the region of the pelvic fin, where it begins to run more towards the dorsal surface, until finally, just behind the supra-orbital crests, it is actually on the dorsal surface (LAT. L., figs. 10B, 11). Between the supra-orbital crests the two lateral canals turn slightly medially and join the supra-temporal canal (S.T.C., fig. 10B) which runs transversely across the head just behind the openings of the endolymphatic ducts.

Running forward from the junction of the lateral line with the supra-temporal and extending forward, a short distance, to join the cephalic canals, is a small canal which Goodrich (1930) maintains is not part of the infra-orbital canal as is usually stated. This temporal canal (T.C., fig. 10B) is innervated by the supra-temporal branch of the glosso-pharyngeal nerve. In *H. portusjacksoni* the buccal branch of the seventh nerve has no ramus oticus, consequently there is no part of the sensory canal which can be called the otic region.

The remaining sensory canals are all in the head region and comprise the supra- and infra-orbital canals, the hyomandibular and mandibular canals.

The supra-orbital canal (S.O.C., figs. 10B, 11) runs from the temporal canal towards the snout, medial to the supra-orbital crest. On the tip of the snout, each supra-orbital canal curves slightly inwards, towards the mid line, and then runs outward around the nasal capsule to join the infra-orbital canal in the region of the superior oral fold of the upper lip. This canal also has a branch which runs from the loop in front of the nasal aperture towards the middle of the central part of the upper lip where it joins the infra-orbital canal from its own side of the body and also the supra- and infra-orbitals of the opposite side. This junction, marked x in figure 10A, corresponds to Garman's median canal (1888) and lies in the skin of the upper lip, just in front of the symphysis of the upper jaw cartilages.

The infra-orbital canal (I.O.C., figs. 11, 12) passes from the temporal canal, behind and below the orbit to the mid-cheek region. Here it curves sharply towards the ventral region and runs a short distance downward. It then turns forward, joining the supra-orbital canal above the superior oral fold of the upper lip. From this junction the infra-orbital canal runs around the side of the nasal capsule to the roof of the mouth, where it turns inward. The canal runs around the back of the excurrent nasal aperture and then forward parallel to the upper jaw till it joins the supra-orbital canal at the point x mentioned above.

The infra-orbital canal gives off another canal which runs backward across the cheek almost to the edge of the first gill-slit. This is the hyomandibular canal (H.C., fig. 11).

Given off ventrally about half-way along the hyomandibular canal is the mandibular sensory canal which runs to the lower jaw. Though extending a considerable distance towards the mid-line, the two mandibular canals do not join up anteriorly (M.C., figs. 10A, 11).

The sensory canals open by pores to the surface of the skin at frequent intervals and they communicate with these pores by means of short tubules (T., figs. 10B, 11). The innervation of the sensory canals is described under the heading of the various branches of the nerves which run to these regions.

Ampullary Organs.—In this shark the ampullary organs are numerous and lie in the integument at a slightly deeper level than the sensory canals. Each organ consists of a pore, which opens to the exterior, connected by a tube-like canal to the sense organ proper or ampulla. The length of the tubules ranges from a few millimetres up to 5 cm. or more in large specimens of *H. portusjacksoni.*

The ampullae, which are all innervated by branches of the seventh cranial nerve, are collected together in *H. portusjacksoni* in knot-like masses much as they are in batoid forms. From these groups of ampullae tubules radiate in many directions (see figures 10A and 11).

In *H. portusjacksoni* five such groups are present. Although Norris (1929) in his paper on the ampullae of Lorenzini stated that in the Centracoidei, as an example of which he took *Heterodontus* (species not stated), there are six distinct groups, I have been unable to find his posterior outer buccal group.

The groups represented are: (1) supra-orbital, (2) inner buccal, (3) outer buccal, (4) hyoidean and (5) mandibular. The hyoidean group is compact and not in three parts in this shark, as Norris stated for his species (1929).

(1) The supra-orbital (S.O.A., figs. 10, 11) group is situated just above the incurrent opening of the nasal organ and is on the extreme tip of the snout. The tubules of the ampullae radiate in all directions and their pores lie around the

border of the nasal aperture on the triangular fold of the upper lip and also on the skin of the antero-dorsal region of the head.

(2) The inner buccal group (I.B.A., figs. 5, 12) is situated under the skin of the roof of the mouth, in the fleshy pad of tissues which lies lateral to the upper jaw cartilage and behind the excurrent opening of the nasal capsule. It has very few ampullae and the tubules are about nine in number. The pores open on this fleshy pad and thus lie in the path of the water flowing out of the nasal capsule into the mouth. The ampullae are innervated by a small branch of the buccal nerve which runs around the outer side of the nasal capsule, beneath the infra-orbital canal, and so on to the roof of the mouth (R.B. VII, fig. 12).

(3) The outer buccal group (O.B.A., fig. 11) lies in the mid-cheek region between the orbit and nasal capsule and is the largest group in this shark. Tubules radiate in many directions to their pores which are distributed partly on the dorso-lateral area of the head in front of the supra-orbital crest; partly in the skin around the nasal capsule and partly to an area of skin below the eye and in front of the spiracle and partly to the lateral fold of the upper lip.

(4) The hyoidean ampullae (HY.A., figs. 10, 11) lie embedded in the integument lateral to the mid-point of the body opposite the hyoid arch. From the ampullae tubules run both dorsally and ventrally, their pores opening in an arc-like series which lies parallel to the hyoid arch. These pores extend from the spiracle to the ventral surface.

(5) The mandibular ampullae (M.A., fig. 10A) are found under the skin of the lower jaw, just behind the lateral lip fold. Their tubules run both forward and backward and their pores are scattered over the skin of this area from the mouth gape as far back as the level of the eyes.

Innervation of the ampullae has been described under the headings of the nerves which supply them.

Spiracular Sense Organ.—There is a small sense organ, associated with the spiracle, which, according to Norris and Hughes (1920), is equivalent to a much modified canal of Lorenzini.

The spiracle, in addition to its straight passage from the exterior to the pharynx, has two blind pouches leading off it, one near its upper end, the other near its lower end. The larger dorsal one leads inward and slightly backward from the external opening towards the wall of the auditory capsule which it almost touches. Nearer its internal opening on its dorso-anterior wall is the smaller ventral diverticulum. The pore of the sense organ opens into this pouch. The organ is innervated by a small branch of the buccal branch of the VIIth nerve. Goodrich (1930, p. 756, figure 732) shows this organ in transverse section in a 70 mm. embryo.

I have been unable to locate any pit-organs in this shark.

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SUMMARY.

The central nervous system and peripheral nervous system of *Heterodontus portusjacksoni* are described, as is also the structure of the pituitary gland.

The nervus terminalis lies on the ventral aspect of the fore-brain in the adult.

The truncus infra-orbitalis in *Heterodontus portusjacksoni* is made up of the maxillary, mandibular and buccal nerves. This condition thus agrees with that found in *Mustelus* (Allis, 1901) and differs from that found in *Squalus acanthias* by Norris and Hughes (1920).

There is no otic branch to the VIIth nerve in *Heterodontus portusjacksoni*.

The description of the ampullary and sensory canals differs slightly from those given by earlier authors.

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